

A RECONSIDERATION OF *SPONDIAS MOMBIN* L. (ANACARDIACEAE)¹

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ABSTRACT

Spondias radlkoferi J. Donn. Sm. is considered distinct from *Spondias mombin* L. It differs chiefly in flowering precociously about one month later than *S. mombin*, in having fewer styles and a fruit which is green at maturity with an oblong endocarp, in having a trunk with a smooth periderm, and in forming droplets of viscid, cloudy sap when slashed. It is most easily recognized by the villous pubescence of its parts.

The genus *Spondias* as treated by Blackwell (1967: 363–367) in the *Flora of Panama* consists of two species, *S. purpurea* L. and *S. mombin* L. Field work done on Barro Colorado Island indicates that another taxon, *S. radlkoferi* J. Donn. Sm., must be segregated from *S. mombin* L.

The occurrence of the segregate taxon was first brought to my attention by Dr. Dennis Knight (University of Wyoming). After he sampled a number of *Spondias* by slashing the trunks, he concluded that two taxa were involved since part of the trees sampled produced small droplets of viscid, cloudy sap shortly after having been slashed, while others did not. He believed the plants to be otherwise quite similar. Robin Foster (Duke University), in the course of his phenological studies on Barro Colorado Island, noted other features which separate *Spondias* into two species. He noted that one group of trees flowers about one month later than do others and that the latter group develop fruits which are elongate and green at maturity. The other *Spondias* trees produce fruits which are more globose and turn yellow, then orange at maturity.

It was not surprising to discover that at least some native Panamanians were already familiar with part of these differences and had called the green-fruited *Spondias* “jobo verde.” Mr. James Zetek wrote, in a recently discovered letter at the Field Museum, to Paul Standley on May 6, 1936 from Barro Colorado Island: “Here we have a mombin that resembles the yellow mombin, but it never gets yellow, it stays green all the time.” He also added, “The trunk of the green one is smooth compared to that of the yellow.”

Recent studies have confirmed the observations of Zetek, Knight, and Foster. Other characters have also been found which further delimit *Spondias mombin* L. and *S. radlkoferi* J. Donn. Sm.

Spondias radlkoferi is readily distinguished from *S. mombin* both in the field and in the herbarium. The former usually flowers about a month later than *S. mombin*, though sufficient overlap occurs in their flowering periods to allow hybridization. Plants of both species may be common in mixed populations on Barro Colorado Islands. However, while they are without question

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closely related species, there is no strong evidence of hybridization. Characters used to separate the two species are numerous and consistent.

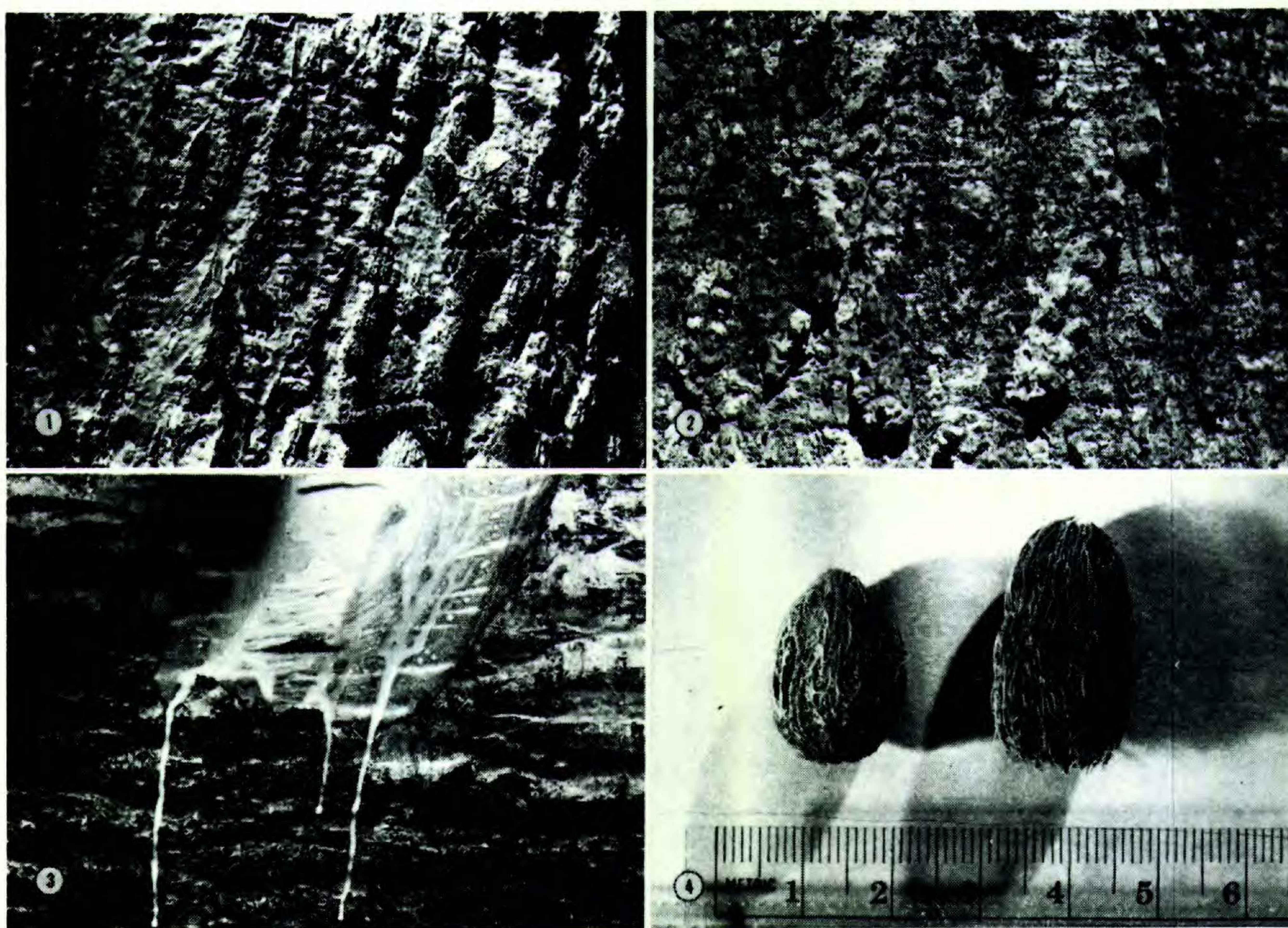
One of the most striking differences between the two species is the precocious flowering of *Spondias radlkoferi*. Although *S. mombin* flowers, on average, about one month earlier than *S. radlkoferi*, it generally has fully developed leaves at time of flowering. *Spondias radlkoferi* begins to flower at about the time new leaves are developing.

No doubt as a consequence of its later flowering, fruits of *Spondias radlkoferi* mature later. Moreover they are somewhat larger. The appearance of their fruit later in the rainy season when food has become slightly more scarce perhaps explains their lack of an attractive color. Whereas *S. mombin* turns orange at maturity and is sweet and tasty, *S. radlkoferi* fruits remain green at maturity and, although edible, they are not sweet and tasty. Their peak of fruiting activity (October-November) comes at a time when competition for food is greatest, so the species has perhaps lost its ability to produce colored fruits or never developed it in the first place. Because of the 3-stylar condition of its flowers, in contrast to the 5-stylar condition of *S. mombin* (discussed later), it is suggested that *S. radlkoferi* has been derived from *S. mombin* and probably has lost its ability to produce colored fruits because the serious competition for food in the late dry season has made attractive fruits unnecessary.

On Barro Colorado Island, larger trees produce the bulk of all animal food. Phenological studies made in central Panama (Croat, 1969) indicate that the peak of the fruiting season for medium- to large-sized trees occurs in April and then tapers off until a low is reached in November when fruit is always very scarce. Since the peak of fruiting for *Spondias radlkoferi* usually occurs during October and November when fruit is most scarce, the species has no difficulty getting an abundance of animals to disperse even its uncolorful, not-so-tasty fruits. The fact that it is apparently as abundant as *S. mombin*, which has attractive, tasty fruits, attests to this.

There are several other good field characters which may be used to separate the two closely related species. The appearance of the bark of the trunk and larger branches offers one of the most characteristic features. While there is some variability from tree to tree, *Spondias radlkoferi* has a trunk with a relatively smooth surface with paper-thin strips of grayish periderm oriented vertically (Fig. 1). The intervening brownish areas are roughened but not raised. In *S. mombin*, the thin grayish strips of periderm are missing and are replaced by much thicker, coarse sections of periderm 1–2 cm wide which are considerably raised from the intervening areas of the trunk (Fig. 2). These thick, irregular patches may contain further elevated, somewhat rounded projections to 7–8 mm high. The intervening area of the trunk is flat but variously fissured in an irregular vertical pattern. Occasionally the lowermost part of the trunk may lack the raised warty strips of periderm. Instead this area usually has a more or less continuous pattern of broad, shallow depressions.

The inner bark of both species is similar. Though quite variable from tree to tree, the inner bark is pink to reddish with whitish, narrowly wedge-shaped areas protruding inward from the periphery (Fig. 3). The surface of the inner



FIGURES 1-4. Comparison of *Spondias mombin* and *Spondias radlkoferi*—1. *S. radlkoferi*, bark showing broad strips of thin periderm.—2. *S. mombin*, bark showing coarse sections of raised periderm.—3. *S. radlkoferi*, slash of trunk showing milky sap flowing from fallen tree.—4. Endocarps of *S. mombin* (left) and *S. radlkoferi* (right).

bark of *Spondias radlkoferi* forms minute, whitish, viscid droplets, easily visible within 30-60 seconds after slashing. Generally the droplets do not increase greatly in size nor do they coalesce or form a stream of sap. However, felled trees may form abundant, runny sap (Fig. 3). In contrast, *S. mombin* shows no evidence of whitish, viscid sap and does not form the small droplets on the inner bark after it has been slashed.

Another distinguishing field character is the appearance of the old fruit endocarps, which generally lie in great abundance beneath trees of both species for most of the year. While some animals, particularly rodents such as the agouti (*Dasyprocta punctata*) and other frugivores, carry many of the fruits away and bury them (Smythe, 1970), monkeys eat the fruit covering in the tree, dropping the inedible endocarp directly to the ground. These weathered endocarps alone are adequate for determination of the tree. The endocarps of *Spondias mombin* are obovoid, 2-2.5 cm long, whereas those of *S. radlkoferi* are oblong, usually 3 cm or more long (Fig. 4).

Those features distinguishing the two species on herbarium specimens are many and varied. The most easily observed definitive character is that of pubescence, although after a number of specimens are examined the color of a dry specimen is adequate for determination. Specimens of *Spondias radlkoferi* dry blackened, while those of *S. mombin* dry greenish. *Spondias mombin*

TABLE 1. Field characters separating *Spondias mombin* L. and *S. radlkoferi* J. Donn. Sm.

<i>S. mombin</i>	<i>S. radlkoferi</i>
Bark very coarse, deeply fissured the intervening corky periderm hard and prominently raised.	Bark not deeply fissured, the strips of periderm paper-thin, smooth.
Slash not producing cloudy, viscid droplets on inner bark.	Slash producing cloudy, viscid droplets within 30–60 seconds on inner bark.
Old endocarps (persisting on ground beneath tree for most of the year) obovoid.	Old endocarps oblong.
Leaves generally fully developed at time of flowering (ca. 1 month earlier than <i>S. radlkoferi</i>).	Leaves usually young at time of flowering.
Mature fruits orange, sweet, and tasty.	Mature fruits green, edible but not very tasty and reported by some to be more acidic.

is sometimes nearly glabrous, but any pubescence consists of short, puberulent trichomes. The species is reasonably uniform throughout its range in this respect, but the trichomes are longer in Mexico. *Spondias radlkoferi* is sparsely to densely villous, especially on the veins of the lower leaf surface and branches of the inflorescence. Trichomes are crisped or straight and are usually curly or at least recurved near the middle.

Although the inflorescence of *Spondias radlkoferi* occurs precociously or nearly so, its flowers do not differ greatly from those of *S. mombin*. The most easily distinguished difference is the generally glabrous pedicel and calyx. This contrasts sharply with the usually densely pubescent branchlets of the inflorescence. Costa Rican and other Central American specimens often have some pubescence on the pedicel, but the trichomes are sparse and long. The pedicel and calyx of *S. mombin* are usually moderately to densely short-puberulent.

In addition there are characters not so easily observed such as shape of the flower buds (ovoid in *Spondias radlkoferi* vs. round to obovoid in *S. mombin*), length of the calyx lobes (much deeper in *S. radlkoferi*), and thickness of the disk. The disk of *S. radlkoferi* is ca. 2.3 mm wide and broader than the width of the stylar clump, whereas the disk of *S. mombin* is only about 1 mm wide and narrower than the stylar clump.

Finally there are significant differences in the number of styles for the two species. *Spondias mombin* generally has 5 styles, less frequently it may have up to half of the flowers with 4 styles and rarely do flowers have only 3 styles. On the other hand, *S. radlkoferi* generally has flowers with 3 or 4 styles (in actual counts of ca. 50 flowers, 60% were 4-stylar and 40% were 3-stylar), very rarely with 5 styles.

There are strong indications that the 3- and 4-stylar conditions have arisen directly from the 5-stylar condition. Analysis of the number of styles on both flowers and juvenile fruits from the same plants invariably shows more fruits with 5 styles than flowers with 5 styles. Since there is no reason to believe that

a flower with 5 styles is more apt to produce fruit than one with 3 or 4, I believe the 4-stylar condition in flowers is often the result of fusion of 2 styles. In a few rare cases the fourth style was seen in the process of pulling apart on a maturing fruit. This is clear evidence that many of the 4-stylar flowers (and for the same reason, the 3-stylar flowers) are the result of a fusion of styles. It is not certain whether fusion of the styles in this manner is detrimental. Both *Spondias mombin* and *S. radlkoferi* appear to have 5-locular fruits, and thus the united styles apparently function as 2 separate styles. The fact remains, however, that the degree of style fusion is more advanced in *S. radlkoferi* than in *S. mombin*.

The characters used in the key were selected because they are usually the easiest to observe on dried herbarium specimens. They are no more definitive however than a variety of other characters. Table 1 lists other sets of contrasting characters useful in separating the two species in the field.

KEY

- Plants glabrous or pubescent parts of plant merely puberulent (the trichomes short and straight); leaves not drying blackened, usually fully developed at time of flowering; blades with a prominent submarginal collecting nerve; calyx pubescent *Spondias mombin* L.
- Plants villous to velutinous (the trichomes not straight or if so long and very dense); leaves usually drying blackened, usually not fully developed at time of flowering; blades lacking a submarginal nerve; calyx glabrous *Spondias radlkoferi* J. Donn. Sm.

***Spondias mombin* L., Sp. Pl. 371. 1753.—“Hogplum.”**

S. lutea L., Sp. Pl., ed. 2. 613. 1762.

S. lutea L. var. *maxima* Engl. in Mart., Fl. Bras. 12(2): 374. 1876.

S. lutea L. var. *glabra* Engl. in Mart., Fl. Bras. 12(2): 374. 1876.

Tree mostly 10–30 m tall, to 60 cm d.b.h.; periderm gray, deeply and coarsely fissured, the raised segments hard, rough, the inner margin irregular; inner bark variously colored, usually with triangular patches of red or tangerine alternating with white; at least the youngest branchlets puberulent. *Leaves* imparipinnate, alternate, to 60 cm long (to 70 cm on juveniles); petiole and rachis usually finely puberulent; leaflets mostly (3–)9–17, opposite or subopposite; petiolules 6–9(–14) mm long; blades oblong to ovate, usually acuminate, acute to rounded and asymmetrical at base, 3–20 cm long and 1.5–7 cm wide, usually \pm glabrous except for puberulence on midribs and major veins above and below; reticulate nerves prominulous, the margin minutely revolute with a prominent submarginal nerve; the larger leaflets with the midrib arched. *Panicles* terminal, to 60 cm long; branches, peduncles, pedicels and calyces usually puberulent; *flowers* 5–7 mm wide, 5-parted, globular to obovoid in bud; pedicels 1–5 mm long, usually articulate near the base; calyx shallow, the lobes short, triangular, sharply acute, usually minutely puberulent, the margins ciliate; petals white, acute and inflexed-apiculate at apex, somewhat reflexed at anthesis; stamens 10, exserted, 1.5–3 mm long, alternating with the fleshy, undulate segments of the disk; disk fleshy, undulate-lobed, to ca. 1 mm wide, the width of one side less than the width of the clump of styles; styles usually 4 or 5 (rarely 3), much shorter than stamens at anthesis, the stigma linear, on the dorsal surface

near apex. *Fruit* oblong to obovoid, 2.5–3 cm long, yellow to orange at maturity; mesocarp to 6 mm thick, fleshy, sweet and tasty; endocarps obovoid, 2–2.5 cm long, hard, covered by a tough, coarse, fibrous matrix.

Flowering principally from March to June (rarely earlier), but most abundant in April and May. Fruits are mature from July to October, mostly in August and September. Leaves are lost during the early part of the dry season beginning in December and January and are replaced before flowering commences.

Throughout tropical America. Introduced in tropical Africa. In Panama principally from tropical moist forest in the Canal Zone and the Provinces of Bocas del Toro, Colón, Panamá and Darién; also known from premontane moist forest in Panamá Province (Farfan Beach), tropical dry forest in Coclé and premontane wet forest in Chiriquí (Progreso).

Since *S. mombin* and *S. radlkoferi* were lumped in the *Flora of Panama* (Blackwell, 1967: 363–367), the following list of exsiccatae from Panama is published here for clarification.

PANAMÁ. BOCAS DEL TORO: Forest above railroad station 7.5 mi., *Croat & Porter 14622* (MO). CANAL ZONE: Along K-2 Highway N of Cocolí, *Croat 9169* (MO). Gaillard Highway on road to treatment plant, *Croat 14015* (MO). Along road between Gatún locks and Fort Sherman, *Croat & Porter 15383* (MO). Road C2c on Cerro Luisa, *Croat 10770* (MO). U.S. Army Tropic Test Center, Miraflores Bridge, *Dwyer & Robyns 3* (MO). Farfan Beach, roadside thicket adjacent to beach, *Dwyer et al. 4688* (MO, F). Summit Garden, *Croat 14481* (MO). Along canal near Gamboa gate to Pipeline Road, *Croat 14836* (MO). Curundu Survival School area, *Tyson & Dwyer 4457* (MO). Miraflores Lake near water plant, *Tyson 3553* (MO). Albbrook, U.S. Army Tropic Test Center side, *Dwyer & Robyns 61* (MO). Near Fort Clayton, *Croat 14462* (MO). Victoria Fill near Miraflores Locks, *P. H. Allen 1762* (MO, F). West of Gamboa, *Haines 571* (MO, F). Edge of lake below spillway on Miraflores Dam, *Stern et al. 1* (MO). Opposite motor pool at Fort Davis, *Lazor & Blum 5413* (MO). Balboa, *Zetek 3611* (MO). Barro Colorado Island, shore of large cove between Slothia Island and Colorado Point, *Croat 6043* (MO); eastern side of Peña Blanca Peninsula, *Croat 5357* (MO); Donato Start, *Croat 5895* (MO); shoreline of Gigante Bay north of Burrunga Point, *Croat 8432* (MO); laboratory clearing near dock, *Croat 10751* (MO); forest north of clearing, *Croat 14090* (MO); Lutz Trail 500, *Croat 11698* (MO); Barbour Trail 700, *Croat 11827* (MO); without further locality, *Carpenter 52* (F, MO); *Zetek 3611* (MO, F). CHIRIQUÍ: Progreso, *Cooper & Slater 207* (MO, F). COCLÉ: Santa Clara Beach, *Croat 9599* (MO). COLÓN: Buenavista, *Holdridge 6390* (MO). DARIÉN: Río Pirre 2–5 mi. above El Real, *Duke 5079*. Trail between Pinogana and Yavisa, *Allen 272* (MO). Santa Fé, *Duke 8400* (MO). Río Pirre, *Croat & Porter 15485* (MO). PANAMÁ: Sajalices, Capira, *E. A. Lao 62* (MO). Pedro Gonzales, Perlas Islands, *P. H. Allen 2598* (MO). Coronado Beach 6 mi. E of San Carlos, *Croat 14260*. Las Lajas, Las Cumbres, *S. A. Sandoval 15* (MO). 1 mi. E of El Llano, *Croat 14484* (MO).

Spondias radlkoferi J. Donn. Sm., Bot. Gaz. (Crawfordsville) 16: 194. 1891.

S. nigrescens Pittier, Contr. U. S. Natl. Herb. 18: 75. 1914.

Tree to 30 m tall, to 75 cm d.b.h.; periderm not deeply fissured, the surface with thin, narrow strips of periderm; inner bark similar to *S. mombin* except producing whitish, viscid droplets within a short time after being cut; younger branches glabrate to sparsely crisp-villous to densely villous, becoming glabrate. *Leaves* imparipinnate, alternate, to 54 cm long, usually sparsely crisp-villous on petiole, rachis, upper midrib and lower surface of leaflets, especially on younger leaves; leaflets mostly 7–19; blades ovate to oblong-elliptic or oblong, abruptly long acuminate, acute to subcordate and markedly inequilateral at base, 2.5–16 cm long and 1.8–6 cm wide, the margins \pm revolute, usually ciliate,

usually lacking a submarginal nerve. *Flowers* 5-parted, usually bisexual, rarely pistillate, the first open flowers usually appearing with the new leaves in terminal and upper axillary panicles to 55 cm long; axes and rarely pedicels sparsely to densely crisp-villous; pedicels glabrous or less often pubescent, articulate usually 0.5–2.5 mm below the calyx (the articulation sometimes obscured by bracteoles); flower buds usually \pm pyriform; calyx cupulate, the lobes thick, prominent, rounded to blunt-triangular, ca. 1 mm long, usually glabrous throughout; petals \pm oblong-elliptic, acute and inflexed-apiculate at apex, 3-nerved (including marginal nerve), 2.3–4.3 mm long, white or greenish-white, recurved at anthesis; stamens 10, 1.7–2 mm long, in 2 series, exerted at anthesis; disk to 2.3 mm wide, fleshy, undulate-lobed, the width of one side more than the width of the clump of styles; ovary subglobose, pubescent; styles usually 3 or 4 (rarely 5), usually free and shorter than the stamens at anthesis in bisexual flowers, the stigmatic surfaces linear, on the dorsal surface near the apex; female flowers rare, the styles to ca. 2 mm long, ca. twice as long as the stamens, united below the middle, the stigmatic surface ovate, turned inward. *Fruit* 3–3.5 cm long, minutely pubescent when immature, oblong to obovate and green at maturity; mesocarp thin, green with a \pm unripened flavor, faintly sweet to acidic; endocarp oblong, nearly as long as fruit, hard, covered by a tough, coarse, fibrous matrix.

Plants often flower 4–6 weeks later than *S. mombin* on Barro Colorado Island, but since their flowering periods overlap, they may be seen flowering together. Flowers occur mostly April to July, especially May and June. Fruits mature from September to December, especially October and November.

Southern Mexico (Veracruz, Chiapas, Campeche), throughout Central America, into Colombia and Venezuela. In Panama known principally from tropical moist forest in the Canal Zone and Panamá Province (El Llano) but also known from tropical moist forest in Bocas del Toro and from premontane wet forest in Chiriquí (Finca Linda to Boquete).

MEXICO. CAMPECHE: Tuxpena, *Lundell* 894 (F, MO). CHIAPAS: Escuintla, *Calculata*, *Matuda* 16668 (F). VERACRUZ: Fortuno, Coatacoalcos River, *Llewellyn Williams* 8694 (MO). YUCATAN: *Gaumer* 24069, 24070 (both F); Southeast Kancabonot, *Gaumer* 23885 (F).

GUATEMALA. ALTA VERAPAZ: Near Alta Verapaz-Petén border, *Steyermark* 45214 (F). CHIRIQUIMULA: Caracol Mts. 1.5 mi. N of Quezaltepeque, *Steyermark* 31408 (F). IAZBAL: Valley of Río Motaqua, *Steyermark* 38348 (F). PETÉN: Camino Melchor K 32, 250 m, *Aquilar* 37 (F). QUETZALTENANGO: Between Colomba and Coatepeque, 850 m, *Steyermark* 52128 (F). RETAHULEU: Region of Ajaxa E of Santa Cruz Mulua, 330 m, *Standley* 88210 (F). SAN MARCOS: Volcán Tajumulco, 1300–1500 m, *Steyermark* 37141 (F). PROVINCE UNKNOWN: Río Dulce, *Wilson* 409 (F).

BELIZE. Corozal-San Antonio Road, *Gentle* 130 (F), *Lundell* 424 (F), 5017 (F, MO), *Wm. C. Meyer* 190 (F). Honey Camp, Orange Walk, *Lundell* 116 (F).

HONDURAS. ATLANTIDA: Forest back of Ceiba, *Yuncker et al.* 8592 (F). CORTES: La Lima, *Williams & Molina* 14467 (F). Río Lindo, *Molina* 5668 (F). MORAZAN: Road between El Jicarto and El Pedregal, *Standley* 14505 (F). Quebrada de la Pita near Zamarano, *Williams & Molina* 14083 (F). Río Yeguaré, 960 m, *Williams & Molina* 13248 (F). Vicinity of Zamarano, *Standley* 13051 (F).

NICARAGUA. Region of Braggman's Bluff, *Englesing* 232 (F).

EL SALVADOR. *Allen & van Severen* 6890 (F).

COSTA RICA. ALAHUELA: La Garita Dam, *Lent* 1148 (F). GUANACASTE: Catalina, *H. E. Stork* 2763 (MO). Comelco Ranch, 7 km NW of Bagaces, *E. R. Heithaus* 119 (MO). Finca la Pacifica, 2 mi. N of Canas, *Gentry* 842, 843 (both MO).

PANAMA. BOCAS DEL TORO: Bocas del Toro, *Dunlap* 504 (MO). CANAL ZONE: Barro

Colorado Island, *Aviles* 10 (MO), *Croat* 4912, 4929, 6040, 6453, 6838, 9046, 9101, 9283, 10082, 10218, 10227, 10294, 10320, 10328, 10836, 11157, 11682, 12580, 14404a (all MO), *Dwyer* 1458 (MO), *Ebinger* 392 (F), *Foster* 861, 1652 (both MO), *Knight* 69–31 (MO), *Shattuck* 82 (F, MO), *Starry* 106 (MO), 107 (F), *Zetek* 3414, 3584, 3645 (all F, MO), 3854, 4998 (both MO). Gaillard Highway near Gamboa, *Croat* 14476 (MO). Gaillard Highway near Summit Garden *Croat* 14830 (MO). Road to Gamboa airport *Croat* 14841 (MO). Along canal near gate to Pipeline Road, *Croat* 14837 (MO). Pipeline Road near gate, *Croat* 16681 (MO). 2 mi. E of El Llano, *Tyson* 1757 (MO). CHIRIQUÍ: Finca Lerida to Boquete, ca. 1300–1700 m, *Woodson et al.* 1109 (MO). PANAMÁ: Vicinity of El Llano, *Duke* 5869 (MO). VENEZUELA. Without exact locality, *Birschel* s.n. (F).

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